WINTER DISTRIBUTION OF AGE AND SEX CLASSES IN AN IRRUPTIVE MIGRANT, THE EVENING GROSBEAK (*COCCOTHRAUSTES VESPERTINUS*)[1]

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Abstract. I used bird–banding data (1955–1988) and logistic regression analyses to test the prediction that male Evening Grosbeaks (*Coccothraustes v. vespertinus*) winter farther north than females, and to investigate whether age groups (first-winter vs. older) differ in their winter distribution. Males wintered farther north than females in 28 of 31 winters in eastern North America (<85°W), and in 12 of 31 winters in central regions. Males typically comprised 53–65% of individuals wintering at the northern edge of the winter range, and 18–27% in the south. No differences in distribution between age classes were observed. Differential migration of the sexes in this species is most likely related to social dominance behavior or to the ability of the larger-bodied males to tolerate harsh winter conditions in northern regions.

Key words: Evening Grosbeak; Coccothraustes vespertinus; irruptions; differential migration; sex; winter distribution.

INTRODUCTION

Although a bird species may be described as being migratory or non-migratory, individuals within a species often pursue different migratory strategies. In some species, certain individuals remain year-round on the breeding grounds, while others move to more southerly latitudes for the winter ("partial" migrants). In others, most individuals leave the breeding grounds during winter, but the distance moved differs among individuals ("differential" migrants; Gauthreaux 1982; Ketterson and Nolan 1983, 1985). In addition, migrations may not occur with annual regularity. In "irruptive" migrants, extensive migration may occur in some winters, but not in others. Irruptions may occur in both partial (e.g., Blue Tit *Parus caeruleus*, Smith and Nilsson 1987) and differential (e.g., Snowy Owl *Nyctea scandiaca*, Kerlinger and Lein 1986) migrant species.

The tendency to migrate is often associated with differences in age and gender. In most partial migrants, females and immature (first-winter) individuals tend to be migratory, whereas males and adults (second-winter or older) tend to be sedentary (Lack 1944, Gauthreaux 1982, Ketterson and Nolan 1985, Smith and Nilsson 1987). The pattern in differential migrants is more complex. Like partial migrants, males tend to winter north of females (Ketterson and Nolan 1976, 1985; Gauthreaux 1982), although the opposite trend is observed in the Snowy Owl (Kerlinger and Lein 1986) and in first-year Sanderlings (*Calidris alba*, Myers 1981). Adults tend to migrate the shortest distances in most irruptive (Svardson 1957, Gauthreaux 1982) and annual-migrant (Gauthreaux 1978, 1982) species studied to date. This pattern is apparently reversed in several emberizine and fringillid finches that migrate with annual regularity, with adults tending to be more migratory than immatures (Ketterson and Nolan 1983, Morton 1984, Prescott and Middleton 1990).

The present study uses continent-wide bird-banding data to document the sex- and age-specific winter distribution of a North American fringillid finch, the Evening Grosbeak (*Coccothraustes vespertinus*). This species is an irruptive migrant (Bock and Lepthien 1976), and in some years migrates from its breeding grounds in the boreal forests as far south as the Gulf of Mexico (AOU 1983). Parks (1953), Shaub (1963) and Balph and Balph (1976) speculated that female Evening Grosbeaks penetrate farther into the wintering grounds during irruption years than do males. Based on these observations, and the patterns observed in other passerine migrants, I predict that male Evening Grosbeaks should winter farther north than females. Because adults winter

farthest south in other species of North American finches, but apparently not in irruptive species, it is difficult to make *a priori* predictions regarding differences in latitudinal distribution of the age classes. I therefore test the general prediction of differential winter distribution between age classes.

For two reasons, the study is restricted to Evening Grosbeaks occurring east of the continental divide, and presumably belonging to the nominate ("eastern") race, *C. v. vespertinus*. First, populations west of the continental divide are comprised of different subspecies, *C. v. brooksi* and *C. v. montana* (AOU 1957), which appear to inhabit the cordilleran region at all times of the year, and may not be as migratory as eastern birds (Bock and Lepthien 1976, Balph and Lindahl 1978). Second, latitudinal migrations by *brooksi* and *montana*, if they occur, would be complicated by the effects of altitude. The geographic restriction aims to minimize altitudinal and subspecific influences on the choice of wintering latitude by Evening Grosbeaks.

METHODS

Computerized records of Evening Grosbeaks banded between 1955 and 1988 were obtained from the Canadian Wildlife Service, Ottawa. All records with status codes indicating that birds were transported, maintained in captivity or released in poor health were eliminated from the database. Records of birds banded in provinces and states west of and including BC, MT, WY, CO and NM were also eliminated (i.e., birds presumably belonging to *C. v. brooksi* and *montana*). Records obtained during the breeding season (1 June–31 August) were excluded. Preliminary analysis of the remaining data indicated that 97.8% of all birds were of known sex. Unsexed birds were omitted from further analyses. Data from all available years were used to investigate sexual differences in winter distribution. However, because criteria for aging Evening Grosbeaks were developed only recently (Yunick 1977), only data from 1977–1978 to 1987–1988 were used to test for age differences in distribution during winter. Individuals were aged as being either "immature" (first-winter) or "adult" (second-winter or older).

The first step in the analysis was to determine the period of the nonbreeding season during which the latitudinal distribution of Evening Grosbeaks reaches its southernmost point, and remains relatively stable (i.e., elimination of migrating individuals). To this end, I calculated the 25% quantile (Q25) latitude (i.e., the latitude north of which 75% of all grosbeaks were banded) for birds of all age and sex classes for half-month periods during each migration year from 1960–1961 to 1986–1987. Migration years between 1955–1956 and 1959–1960 were eliminated from this analysis because banding data were available only as monthly summaries during this period. The mean Q25 latitude for each half-month period was then calculated for all years. The period during which the latitudinal distribution of nonbreeding populations stabilizes was then subjectively determined. This period, hereafter referred to as "winter," was used in all subsequent analyses of sex and age distribution.

Because of the binary nature of the dependent variables (age and sex), logistic regressions (Neter et al. 1985) were used to test the prediction that male Evening Grosbeaks winter farther north than females, and to investigate age differences in winter distribution. For each winter, the total numbers of birds of each sex and age were calculated in each 10-min latitude/longitude block (blocks containing <5 birds of known age or sex were omitted). The proportion of males, or adults within each sex was calculated using the logit transformation, logodds = $\ln[p/(1 - p)]$, where $p = n/N$ if $0 < n < N$; $p = 0.5N$ if $n = 0$; and $p = 1 - (0.5N)$ if $n = N$ (where n = number of males or adults, and N = total number sexed or aged within each sex). Logit-transformed proportions were then included as dependent variables in a multiple regression with year (YEAR), latitude (LAT) and longitude (LONG) as independent variables. Proportions were weighted by $w = Np(1 - p)$ to adjust for inequalities in the variances of the error terms (Neter et al. 1985). When appropriate, the number of interaction and main effects in the regression model was reduced by backward elimination of terms (Neter et al. 1985). After testing for annual and longitudinal effects, predicted proportions of males and adults of each sex were calculated from $p = e^{a + b[LAT]}/1 + e^{a + b[LAT]}$, where a and b are the intercept and slope estimated from the regression of logodds sex or age against latitude.

RESULTS

The analysis of movements of grosbeak populations during the nonbreeding season included 544,666 individuals of known sex (0.82 male:1
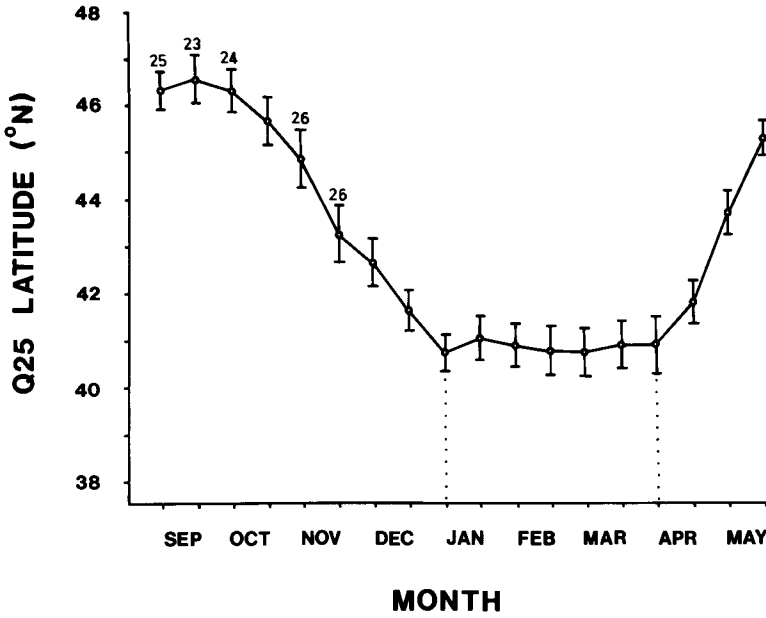
FIGURE 1.   Mean Q25 latitude (±SE) by half-month periods between 1 September and 31 May, 1960–1961 to 1987–1988. Numbers on error bars represent number of years used in calculation of mean values, if <27.
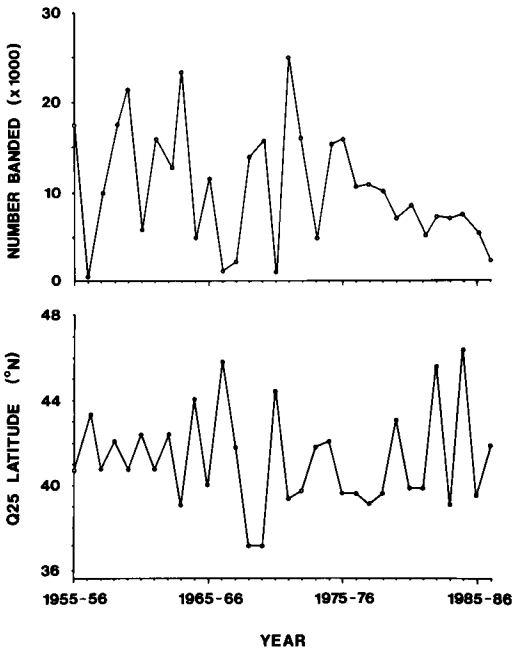

FIGURE 2.   Number of Evening Grosbeaks banded (top), and Q25 latitude of grosbeak populations (bottom) during winter, 1955–1956 to 1987–1988.

female; annual range, 0.54:1 to 1.31:1). Birds reach the southernmost latitude by early January, and remain there until the northward migration begins in mid-April (Fig. 1). Thus, "winter" is the period between 1 January and 15 April for all subsequent analyses. Because records obtained between 1955 and 1959 were summarized on a monthly basis, "winter" during 1955–1956 to 1958–1959 was considered to be January–March, inclusive. Figure 2 provides the sample size and Q25 latitude for each winter, emphasizing the annual variability of Evening Grosbeak migrations.

SEX DISTRIBUTION

A total of 336,318 grosbeaks (61.7% of total sample) of known sex (0.77:1 male:female; annual range 0.48:1 to 1.19:1) were banded during the winter. Logistic regression indicated a significant YEAR*LAT*LONG interaction effect on the proportion of wintering males ($F_{30, 3107} = 3.80$, $P < 0.0001$). To clarify the longitudinal effect, the analysis was repeated within each of two longitudinal regions: "east" (<85°W) and "central" (≥85°W). In both regions, there was a significant YEAR·LAT effect (east: $F_{31, 2506} = 7.16$, $P < 0.0001$; central: $F_{30, 601} = 2.23$, $P < 0.0002$). Re-
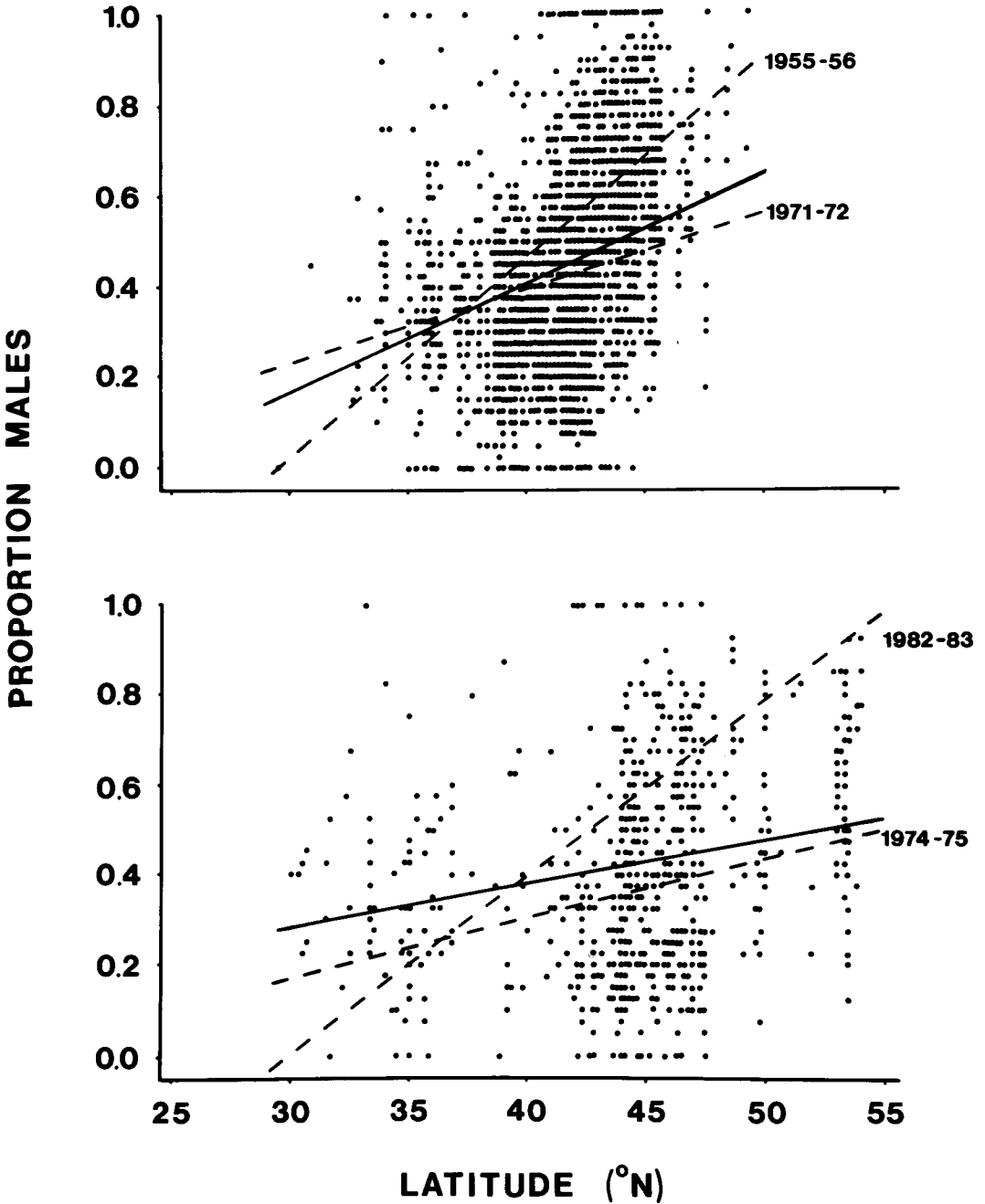
FIGURE 3.   Overall regressions (solid line), and minimum and maximum annual slopes (dashed lines) of logit-transformed proportion of males vs. latitude in eastern (top) and central (bottom) North America.

gression slopes were significantly greater than 0 ($P < 0.05$, one-tailed tests) in 28 of 31 years in the east, and in 12 of 31 years in the central region. The overall regression of logodds sex on latitude (east: logodds Y = $-4.66 + 0.11$[LAT], $F_{1, 2568} = 558.7$, $P < 0.0001$; central: logodds Y $= -2.32 + 0.04$[LAT], $F_{1, 662} = 53.97$, $P < 0.0001$), along with minimum and maximum an-

nual slopes are shown in Figure 3. Over all years, the predicted proportion of males in the eastern region declined from 65% in the north (50°N) to 18% in the south (30°N). In the central region, the proportion of males declined from 53% at 55°N to 27% at 30°N.

AGE DISTRIBUTION

During the winters of 1977–1978 to 1987–1988, 15,857 males (53.9% of total) and 7,190 females (16.9%) of known age were reported. The overall age ratio (adult : immature) was 0.96:1 for males (range, 0.69 to 1.32:1), and 0.66:1 for females (range, 0.39 to 1.16:1).

Following the elimination of insignificant terms, the regression model for both sexes reduced to contain LAT, YEAR and their interaction (males: $F_{19, 329} = 1.57$, $P = 0.06$; females: $F_{19, 147} = 1.77$, $P = 0.03$). Regression slopes for males were significantly different from 0 (two-tailed tests) only in 1982–1983 ($F_{1, 19} = 8.53$, $P < 0.0001$), when the proportion of adults increased with latitude (logodds Y = -11.73 + 0.26[LAT]). For females, only the regression slope for 1984–1985 was significantly different from 0 ($F_{1, 12} = 13.46$, $P = 0.003$), when the proportion of adults decreased with increasing latitude (logodds Y = $15.93 - 0.07$[LAT]).

DISCUSSION

Despite the annual variability in Evening Grosbeak migrations, male grosbeaks, like other North American finches (King et al. 1965, Ketterson and Nolan 1976, Morton 1984, Prescott and Middleton 1990), tend to winter farther north than females. However, evidence for distributional differences between the age classes is equivocal. First-winter Evening Grosbeaks of both sexes show no tendency to migrate farther than adults as reported for other irruptive species (Svardson 1957, Gauthreaux 1982, Kerlinger and Lein 1986), nor to winter farther north like non-irruptive finch species (Ketterson and Nolan 1983, Morton 1984, Prescott and Middleton 1990).

Three hypotheses have been proposed to account for the tendency for age and sex classes to be non-randomly distributed over a latitudinal gradient during winter (reviewed in Myers 1981, Ketterson and Nolan 1983). The arrival time hypothesis states that if there is strong intrasexual competition for mates, there may be sexual differences in the advantages of early arrival on the breeding grounds in spring. The sex that establishes territories (usually males) to acquire mates should benefit most from early arrival, and this may be achieved by wintering farther north. The social dominance hypothesis states that when there is individual variation in competitive ability during the non-breeding season, socially subordinate individuals may be forced to make longer migrations to avoid competition with dominants. The body size hypothesis considers that larger-bodied individuals (or sex and age classes) should remain farthest north, because their smaller surface area to body-volume ratio and lower mass-specific metabolic rate (Kendeigh 1945, Calder 1974) enhance tolerance to cold temperatures and periods of food shortage. Such conditions are presumably most common in northern parts of the winter range.

Our current knowledge of the biology of Evening Grosbeaks is scant, and a full evaluation of the above hypotheses is not presently possible. However, evidence suggests that the arrival time hypothesis should not influence the winter distribution of sex classes in the Evening Grosbeak. Neither males nor females of this species are territorial during the breeding season (Bekoff and Scott 1989), and observations of courtship on the wintering grounds during April and May (Shaub 1956, 1963; Downs 1958) suggest that pairbonds may be formed well before spring migration is completed. The timing and location of pair formation therefore suggests that males do not winter farther north than females to gain early access to mates in the spring.

The importance of social dominance in the regulation of distance migrated from the breeding grounds may be especially applicable to gregarious species like the Evening Grosbeak, where nonbreeding flocks may contain up to several hundred individuals, and intraspecific aggression is frequently intense (Bekoff and Scott 1989). Male grosbeaks are socially dominant over females at feeders (Balph and Balph 1976, Bekoff and Scott 1989, pers. obs.), which is consistent with the social dominance hypothesis. The dominance status of immatures relative to adults during winter is unknown, but the absence of differences in winter distribution between age classes predicts that there should be no difference in dominance status between immatures and adults of the same sex. If the dominance hypothesis is true, it must also be shown that low ranking grosbeaks are at an energetic or survival disadvantage relative to

dominants, and migrate farther south to avoid competition.

Based on the known winter distribution of the age and sex classes, the body size hypothesis predicts that immatures and adults should be of equal body size, but that males should be larger than females. There are no data on relative body size of the age groups, but males are both longer-winged and heavier than females (Balph 1976, Lago 1979) which is consistent with the hypothesis. There is also no information on whether male grosbeaks experience a survival advantage during inclement conditions, and whether this advantage results from their larger size. However, there is evidence from other species that large size can be advantageous during winter. Large-bodied individuals are known to fast for longer periods in the laboratory (Ivacic and Labisky 1973, Ketterson and King 1977, Ketterson and Nolan 1978) and are more likely to be recaptured following periods of inclement weather (Fleischer and Johnston 1984, Lehikoinen 1986). However, higher survivorship of large-bodied birds in the wild need not result from metabolic advantages. These individuals may survive better because size can be a determinant of dominance rank (Baker and Fox 1978, Richner 1989) and birds of high dominance rank have better access to food sources (Baker et al. 1981, Ekman and Askenmo 1984).

Why is differential migration of the sexes more pronounced in eastern than in central North America? If differences in body size are a factor in the selection of wintering latitude, then conditions in the east must either be colder, or food supplies more unpredictable than in central regions. If social dominance is important, then intraspecific competition must be more intense in the east. Long-term, mean air temperatures recorded during January show that locations in the east average 1–3°C warmer than comparable latitudes in the central region (Bryson and Hare 1974), which is inconsistent with the body size hypothesis. Evening Grosbeaks winter in higher numbers in the east (e.g., Fig. 3, but see Root 1988), suggesting that competition may be more intense in this area. Unfortunately, information on regional differences in the predictability and abundance of food, necessary for a full evaluation of both the body size and social dominance hypotheses are not available.

This study adds the Evening Grosbeak to the ever-increasing list of North American migrants that show age or sex differences in winter distribution and suggests that irruptive migrations need not be predominantly by first-year birds, as suggested for other species (Svardson 1957, Gauthreaux 1982). Clearly, more work is required before an explanation for differential migration by sex classes of the Evening Grosbeak can be offered, but future research into the body size and social dominance hypotheses may prove to be the most fruitful approach to understanding the regulation of migratory distance in this species.

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